CHAPTER 2-4
PROTOZOA: RHIZOPOD ECOLOGY

TABLE OF CONTENTS

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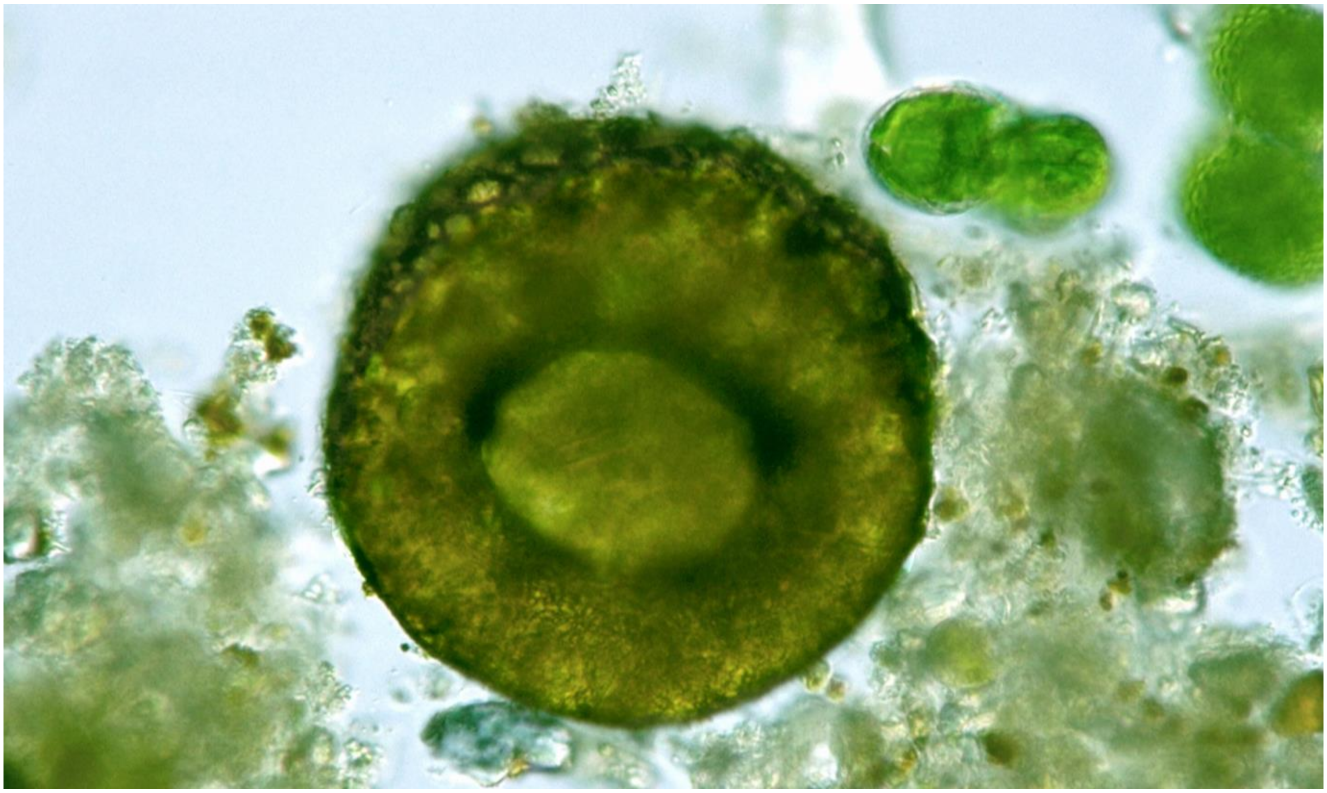

Figure 1. Test of ***Centropyxis ecornis*** with desmids that are common cohabitants in peatlands. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Geographic Distribution

Testate amoeba communities not only are diverse in themselves, but they typically occur with a diversity of algae and other micro-organisms (Figure 1). Moss-dwelling testate amoebae have been reported from the Antarctic (*e.g.* Richters 1904, 1908a, b; Sudzuki 1964; Smith 1973a, b, c, 1974a, b, 1986; Beyens *et al*. 1988; Balik 1994), to The Czech Republic (Balik 2001), to the Canadian Arctic (Beyens *et al*. 1986a, b), to name only a few. Beyens and Chardez (1994) thought that the amoebae formed specific assemblages related to the moss habitats. Working in the Mt. Kurikoma district of Japan, Chiba and Kato (1969) likewise suggested that the testacean community structure is related to the bryophyte habitat.

Bartos (1949) reported on the moss-dwelling Rhizopoda of Switzerland. Most of his samples were from aerial mosses, but the Rhizopoda belonged to damp moss associations. The largest numbers of individuals belonged to the testate amoeba genus ***Centropyxis***, including ***C. aerophila*** (Figure 3), ***C. eurystoma***, ***C. kahli***, and ***C. ecornis*** (Figure 4), in all the mosses. Smith (1992) reported ***Arcella arenaria*** (Figure 2), ***Centropyxis aerophila*** (Figure 3), ***Corythion dubium*** (Figure 5), ***Difflugia lucida***, ***Diplochlamys timida***, ***Heleopera petricola*** (Figure 6), and ***Trigonopyxis arcula*** (Figure 7) from Antarctica, where numbers were generally low compared to Northern Hemisphere studies. Only ***Bryum*** exhibited larger populations, those of ***Arcella arenaria***. ***Centropyxis aerophila*** seems to prefer more calcareous situations (Coûteaux 1969), although its distribution in South Georgia (Antarctica) occurs at *p*H 4.5-5.6 (Smith & Headland 1983). This species is variable, whether due to geography or ecology (Chardez 1979).

Figure 2. ***Arcella arenaria***. Photo by Yuuji Tsukii, Protist Information Server, with permission.

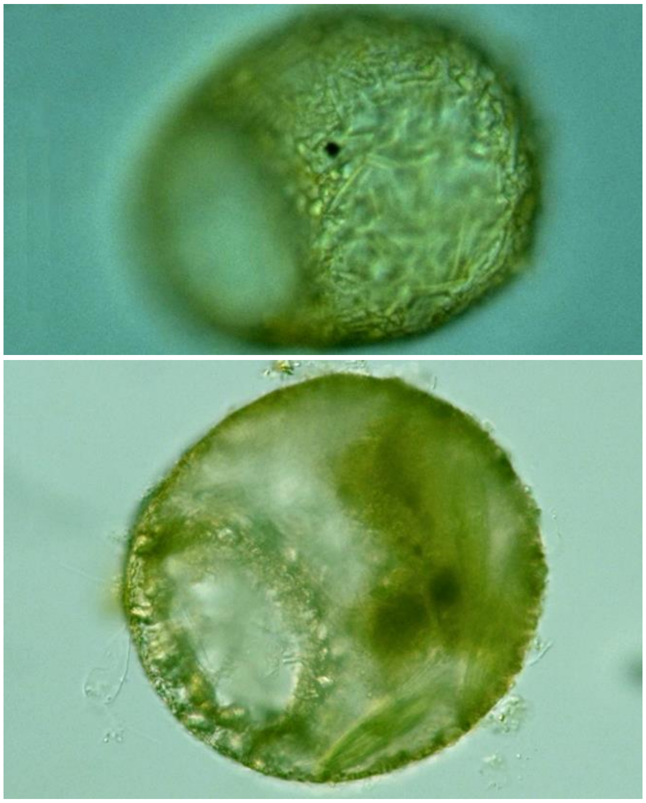

Figure 3. ***Centropyxis aerophila***, an aerial protozoan that lives on damp mosses. Photos by Yuuji Tsukii, Protist Information Server, with permission.

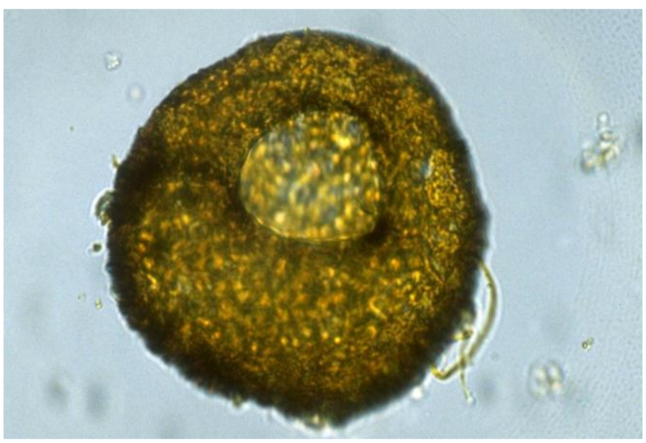

Figure 4. ***Centropyxis ecornis***, a doughnut-shaped testate amoeba that is common among mosses. Photo by Yuuji Tsukii, with permission.

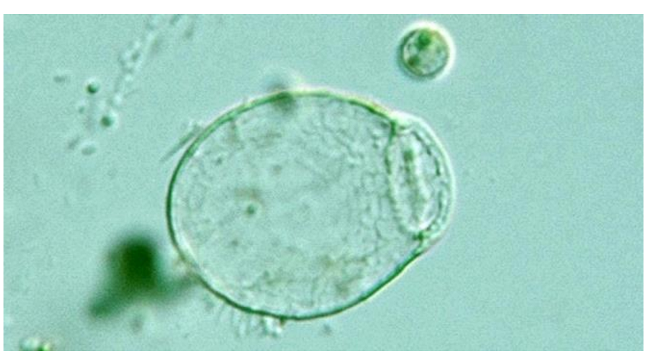

Figure 5. ***Corythion dubium*** test. Photo by Yuuji Tsukii, with permission.

Figure 6. ***Heleopera petricola***. Photo by Yuuji Tsukii, Protist Information Server, with permission.

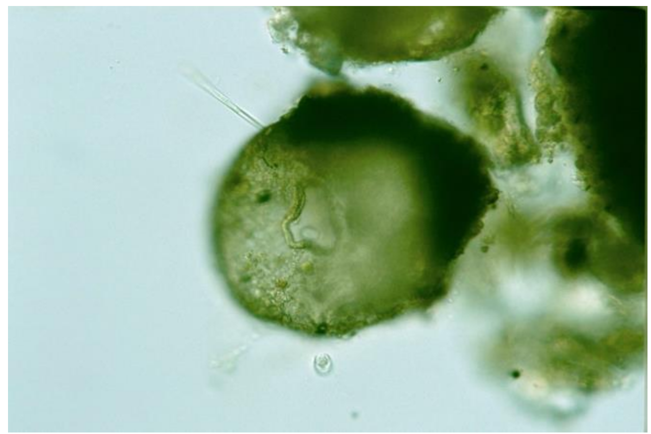

Figure 7. ***Trigonopyxis arcula***. Photo by Yuuji Tsukii, Protist Information Server, with permission.

As for most of the invertebrates, the highest numbers seem to occur in peatlands. Gilbert *et al.* (2003) reported 29,582 ± 9650 active individuals per liter of *Nebela vas* and 2263 ± 1620 for the encysted ones at Pradeaux peatland (Puy de Dôme, France), with the greatest abundance at the end of June (almost 40,000), dropping to the lowest number in July (less than 15,000).

Communities

Although most of the information regarding rhizopod communities is for peatlands (Subchapter 2-5), a few studies have discussed communities in other types of bryophytes. Beyens *et al*. (1990) compared communities from the coastal lowlands on Devon Island, NWT, Canadian Arctic. These encompassed 57 taxa on mosses, soils, and lichens. The dry, acidic moss habitats were characterized by ***Assulina muscorum*** – ***Corythion dubium*** assemblages. In wet, neutral *p*H habitats, ***Paraquadrula irregularis*** was dominant. Sedge moss meadows had a soil fauna association of ***Plagiopyxis callida*** – ***Plagiopyxis declivis***. ***Centropyxis minuta*** was mostly on coarsely textured soils in this study, but is known from mosses elsewhere.

Mazei and Belykova (2011) found 29 rhizopod species/forms associated with mosses at the water edge in seven streams of the Sura River basin (Middle Volga region, Russia). The dominant species are ***Centropyxis aerophila***, ***Centropyxis cassis***, ***Crythion dubium***,

Euglypha ciliata glabra, ***Tracheleuglypha dentata***, ***Trinema complanatum***, ***Trinema enchelys***, and ***Trinema lineare***. The species richness in these communities varies from 2 to 11 per sample, with an abundance of 100 to 4000 individuals per gram dry moss. Mazei and Belykova suggested that the character of the community could be influenced by forest cover, water hardness, "biogenic elements," stream size, and environmental contamination.

Davis (1981) reported that the testate rhizopods were the dominatform of non-photosynthetic life among mosses in the maritime Antarctic. Smith (1986) reported ten species on the moss ***Sanionia uncinata***: ***Assulina muscorum***, ***Corythium dubium***, ***Difflugia lucida***, ***Nebela lageniformis***, ***Nebela wailesi***, ***Phryganella acropodia***, ***Trigomopyxis arcula***, and a species of ***Difflugia***, possibly ***D. mica***. The most abundant of these were ***Difflugia lucida*** and ***Assulina muscorum***. The species richness was low, similar to that found in other southern latitudes.

Moisture Relationships

Moisture plays an important role in survivorship. Like many other bryophyte inhabitants, the testate amoebae among the bryophytes survive the wet-dry changes so common among the bryophytes (Chardez 1990). When conditions are dry, many rhizopod amoebae can **encyst** (Sacchi 1888 a, b; Heal 1962), thus escaping the need for water during long periods of drought (Hingley 1993). Some have survived 5-8 years in dry moss (Hingley 1993).

Chlamydomyxa montana is one such encysting protozoan. In its amoeboid state it feeds on diatoms, but it is photosynthetic in bright light in its encysted state (Pearlmutter & Timpano 1984). Cysts of this unusual amoeba occur on the branches of ***Sphagnum*** (Lankester 1896). These cause the moss to be ruddy brown, with a glistening surface due to olive-brown disk-like or ovoid cysts about 1-2 mm in diameter. When these are awakened, a network of threads appears, signifying the amoeboid stage.

In Germany, the death rate of testaceans in the river exceeded that in mats of the terrestrial ***Plagiomnium cuspidatum*** (Figure 8) (3%/day) (Schönborn 1977). This is perhaps due to the greater resistance to desiccation among the terrestrial taxa and represents a time of optimal conditions. With ***Euglypha ciliata*** (Figure 9, Figure 10) (429,000 individuals/m^2; 15.5 mg/m^2) and *Assulina muscorum* (Figure 11) (406,000 individuals/m^2; 2.9 mg/m^2) dominating, the production rate on the mosses is 40,600 individuals m^{-2} day^{-1} and a biomass of 0.3 mg m^{-2} day^{-1}. In drier times, generation time increases as amoebae go dormant, causing fewer generations to be produced and reducing the productivity. Soil organisms spend only half the time for one generation compared to those living on the bryophytes. Not only is the moss subject to more frequent drying, but the number of ***Aufwuchs*** on the mosses is lower, thus providing less food.

Rhizopod communities are determined by the moisture and temperature conditions available to them (Chiba & Kato 1969). This affects not only the clumps of moss they inhabit, but also their vertical distribution within the clump. For example, in the Canadian Arctic, ***Trinema lineare*** (Figure 12) occurs deep in the moss mat where conditions are more humid (Beyens *et al*. 1986b).

Rhizopods are able to inhabit ponds, lakes, marshes, and swamps where there is likewise sufficient moisture to support moss growth (Cash *et al*. 1905). They are constant members of the community near ponds among the mosses ***Drepanocladus*** spp. (*sensu lato*), ***Philonotis fontana***, and ***Aulacomnium palustre***, where they are typically associated with diatoms. Rhizopods also subsist among mosses on tree trunks and roots in shaded forests.

Figure 8. ***Plagiomnium cuspidatum***, a safe site compared to soil. Photo by Michael Lüth, with permission.

Figure 9. ***Euglypha ciliata*** showing the cilia that give it its name. Photo by Yuuji Tsukii, Protist Information Server, with permission.

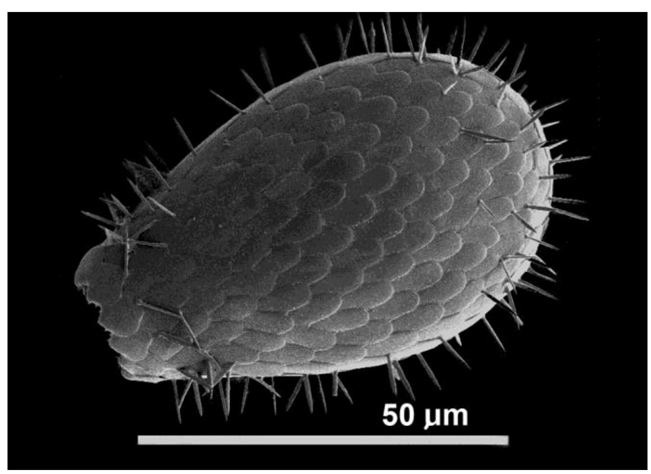

Figure 10. Test of ***Euglypha ciliata***. Photo by Edward Mitchell., with permission

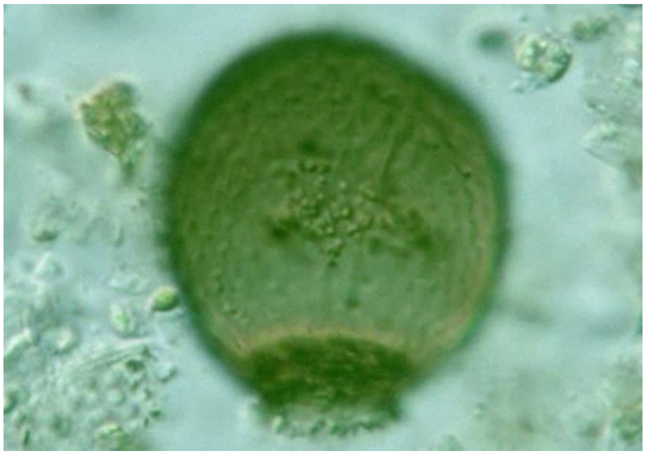

Figure 11. ***Assulina muscorum***, a common bryophyte inhabitant. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Figure 12. ***Trinema lineare***. Photo by Yuuji Tsukii, PIS, with permission.

Bartos (1949) found that in those mosses that were often dry, ***Centropyxis labiata*** occurred, with ***C. platystoma*** and ***C. constricta*** (Figure 13) in somewhat damper ones. The very dry mosses housed ***Trigonopyxis arcula*** (Figure 14) and ***Bullinularia indica*** (Figure 15). Several species occurred in all moss probes: ***Trinema enchelys*** (Figure 16), ***Nebela collaris*** (Figure 17), ***Euglypha ciliata*** (Figure 10), and ***Assulina muscorum*** (Figure 11).

Figure 13. Test of ***Centropyxis constricta***, a common protozoan among damp mosses. Photo by Yuuji Tsukii, with permission.

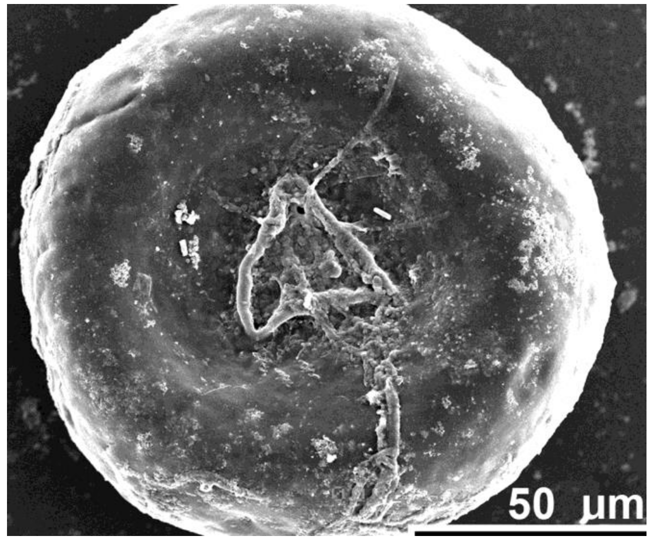

Figure 14. Test of ***Trigonopyxis arcula***. Photo by Edward Mitchell, with permission.

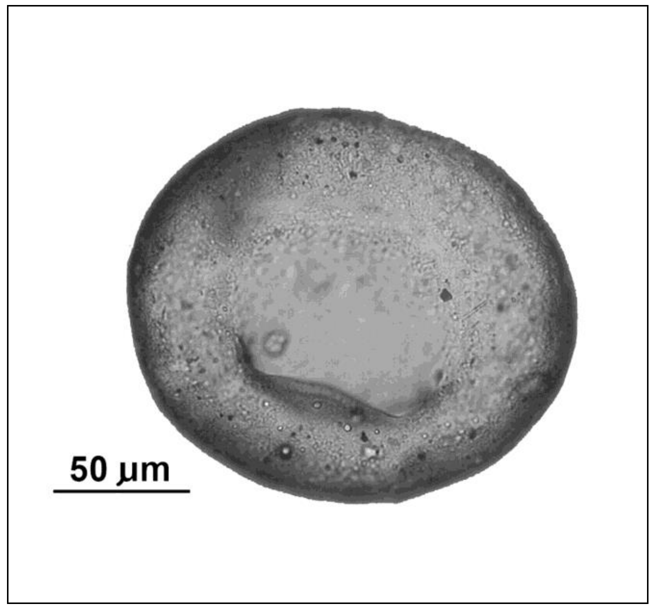

Figure 15. Test of ***Bullinularia indica***, a protozoan that lives on dry mosses. Photo by Edward Mitchell, with permission.

Figure 16. ***Trinema enchelys*** test with living protoplasm. Photo by Yuuji Tsukii, Protist Information Server, with permission.

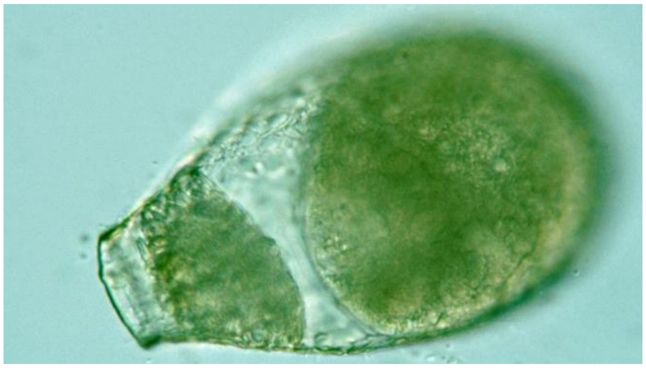

Figure 17. ***Nebela collaris***, a common species among mosses. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Case Building

The large, shell-forming ***Arcella*** is a common genus among bryophytes, particularly ***Sphagnum*** (Hoogenraad & De Groot 1979; Chardez & Beyens 1987). ***Arcella*** builds a case that is completely organic (Meisterfeld & Mitchell 2008; Figure 18) and resembles a tiny doughnut in bottom view (Figure 19). ***Arcella crenulata*** and ***A. mitrata*** (Figure 20) tend to occur together on ***Sphagnum*** that is constantly wet, low in nutrients, and in a *p*H range of 4-6. Others such as ***A. arenaria*** (Figure 19), ***A. catinus*** (Figure 21), ***A. artocrea*** (Figure 22, Figure 23), and ***A. microstoma*** "prefer" ***Sphagnum***, but also occur elsewhere.

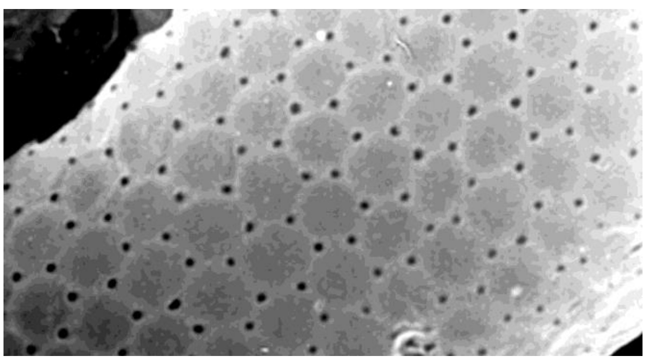

Figure 18. SEM image of test of ***Arcella hemisphaerica*** showing organic construction. Photo by Ralf Meisterfeld, with permission.

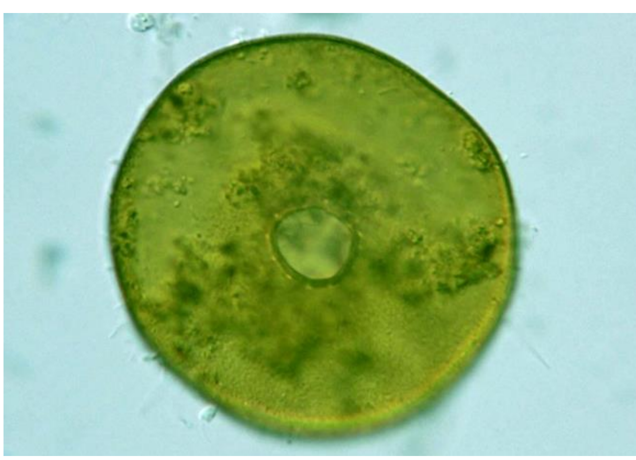

Figure 19. Test of ***Arcella arenaria***. Photo by Yuuji Tsukii, with permission.

Figure 20. Living ***Arcella mitrata***. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Food

The Rhizopoda have long been considered to be bacterivores, but it appears that this conclusion may be somewhat short-sighted. Although most are heterotrophic, a few are mixotrophic, housing photosynthetic algae as symbionts (Gilbert *et al.* 2000). The ability of some taxa to ingest a wide size range (0.2-1000 µm) of organisms and particulate organic matter (POM) offers a potential competitive advantage.

Figure 21. Test of ***Arcella catinus***. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Wilmshurst (1998) found protozoa so common in New Zealand ***Sphagnum*** peatlands that she estimated that more than 50,000 protozoans could "eke out a living" in a gram of fresh moss. The amoebae survive by consuming particulate organic matter, algae that grow epiphytically on the mosses, bacteria, fungi, plant cells, and even smaller amoebae (Richardson 1981; Gilbert *et al*. 2000). Although bacterivorous taxa are the most frequent, some taxa eat algae and other protozoa almost as large as they are.

Deriu *et al.* (1995) challenged earlier studies that suggested that ***Sphagnum*** served as a reservoir of mycobacteria as a food source, citing the medicinal properties of ***Sphagnum*** as evidence of the near absence of mycobacteria. Nevertheless, it is likely that bacteria serve

as the primary food source. Mieczan (2006) found that among the ***Sphagnum*** in Poleski National Park in Poland the bacterivorous protozoa had the greatest numbers, whereas those that ate algae were least common.

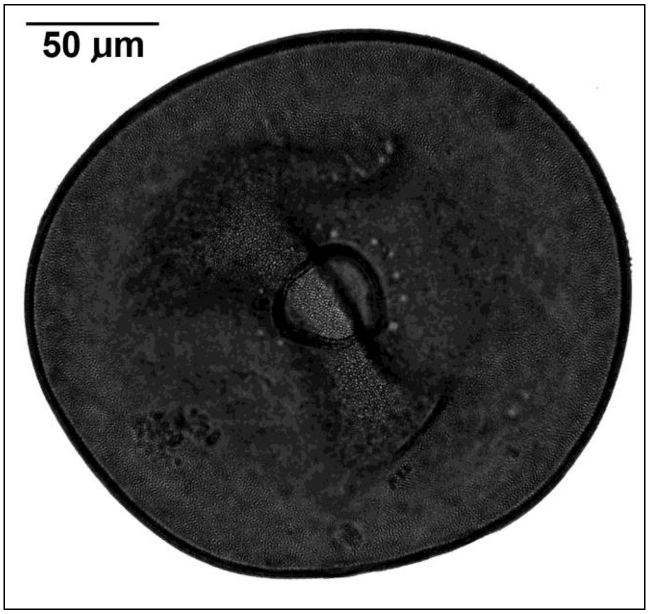

Figure 22. Test of ***Arcella artocrea***. Photo by Edward Mitchell, with permission.

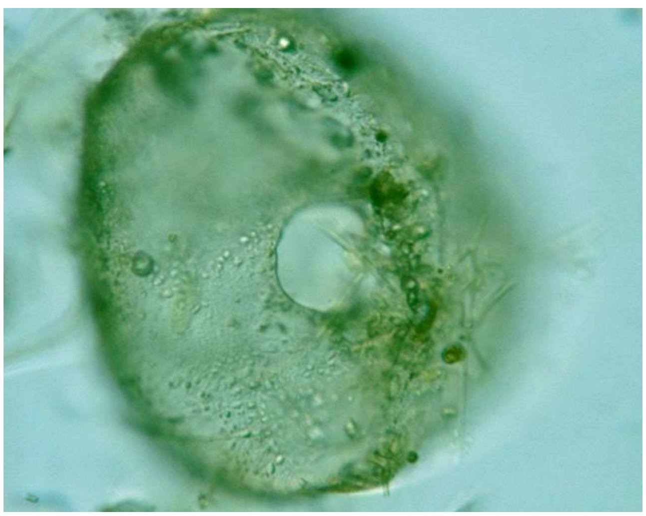

Figure 23. Test of ***Arcella artocrea***. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Symbionts

Despite their habitation within a case or test, some of the Testacea also have **symbionts**. Among those inhabiting bryophytes, symbiotic taxa include ***Amphitrema flavum*** (Figure 24), ***Difflugia oblonga*** (Figure 25), ***Hyalosphenia papilio*** (Figure 26), and ***Heleopera sphagni*** (Figure 27) (Burkholder 1996; Charrière *et al*. 2006; Meisterfeld & Mitchell 2008). Their dependency on light forces them to live in the upper few cm where the algae live both independently and within the rhizopod, and are able to photosynthesize. A more detailed discussion of algal symbionts is in the subchapter on Protozoa Diversity (Chapter 2-1).

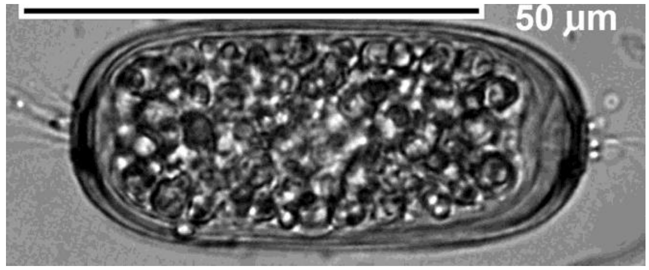

Figure 24. ***Amphitrema flavum***, a protozoan that incorporates green algal symbionts. Photo by Edward Mitchell, with permission.

Figure 25. ***Difflugia oblonga*** with green algae, possibly living as symbionts. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Bryophyte Chemistry

Moss chemistry appears to play an important role in at least some cases in determining species richness. Testate amoebae occupying ***Hylocomium splendens*** (Figure 28) in the Italian Alps were distributed largely in accordance with differences in C, P, Ca, Mg, Al, Fe, and Na of the moss tissues (Mitchell *et al*. 2004). The researchers suggested that the chemistry affected the prey organisms, thus affecting their consumers, the amoebae. Surprisingly, there was no relationship to the important nutrients N and K. Both Mitchell *et al*. (2004) and Bonnet (1973b) concluded that distribution of testate amoebae among wefts of *H. splendens* was independent of soil type.

Figure 26. ***Hyalosphenia papilio*** densely impregnated with symbiotic algae. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Figure 27. ***Heleopera sphagni*** with what appear to be algal symbionts. Photo by Yuuji Tsukii, Protist Information Server, with permission.

In addition to the taxa mentioned above, Mieczan (2006) also found ***Codonella cratera*** (Figure 29) in two Polish peatlands. There is surely a wealth of species waiting to be discovered in the little-explored bryophyte microcosm. Corbet (1973) managed a 38-page article on the testate species of ***Sphagnum*** at a single location, Malham Tarn, Yorkshire. Other bryophytes have received much less attention.

Figure 28. ***Hylocomium splendens***, a terrestrial habitat for protozoa. Photo by Michael Lüth, with permission.

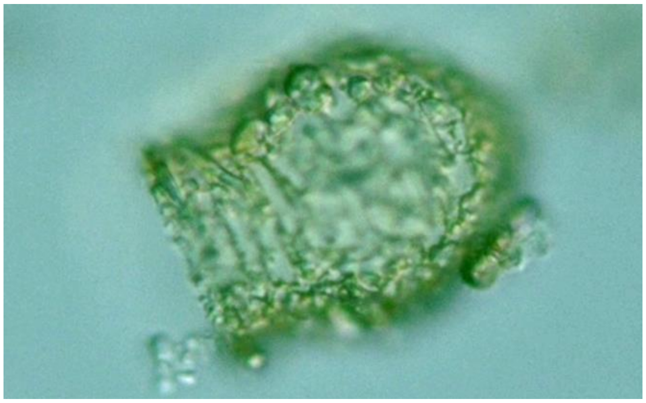

Figure 29. Test of ***Codonella cratera***. Photo by Yuuji Tsukii, Protist Information Server.

Pollution – Heavy Metals

Rhizopods, as well as bryophytes, can serve as indicators of pollution damage to a community. In a study of the moss ***Barbula indica*** in Viet Nam, both richness and abundance of rhizopods were reduced by lead (Nguyen-Viet *et al*. 2007). Shannon diversity was negatively correlated with cadmium. Although several species of rhizopods were negatively correlated with lead, cadmium, zinc, and nickel, lead was the only pollutant that caused a significant change at the community level. Other effects will be discussed in the sub-chapter on Peatland Rhizopods.

Summary

Centropyxis and ***Arcella*** are among the most common of the testate amoebae among epiphytic bryophytes. Communities vary seasonally as moisture changes. Moisture is also the greatest determinant of the choice of bryophyte and vertical location within it, but for some *p*H also plays a role. Construction of cases may help them to survive brief dry periods, but most encyst until favorable moisture returns. Terrestrial taxa are more resistant to desiccation than are aquatic ones. Generation time is longer on mosses because of the time spent encysted.

Many of the rhizopods are bacterivores, but they also consume fungi, algae, plant cells, and smaller amoebae. Chemistry may affect the available food organisms, but N & K do not seem important. Several of the rhizopods harbor ***Chlorella*** as symbionts. Their need for light causes these taxa to live in the upper few cm of the bryophyte layer.

Rhizopods often have a negative correlation with pollutants, especially some of the heavy metals.

Acknowledgments

Yuuji Tsukii was most helpful in giving me permission to use his images from the Protist Information Server. Edward Mitchell helped me to find literature and provided me with a number of images I couldn't find elsewhere.

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